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The carnivore remains from the Sima de los Huesos Middle Pleistocene site (Sierra de Atapuerca, Spain)

Remains of carnivores from the Sima de los Huesos site representing at least 158 adult individuals of a primitive (i.e., not very speleoid) form of *Ursus deningeri* Von Reichenau 1906, have been recovered through the 1995 field season. These new finds extend our knowledge of this group in the Sierra de Atapuerca Middle Pleistocene. Material previously classified as Cuoninae indet. is now assigned to *Canis lupus* and a third metatarsal assigned in 1987 to *Panthera* cf. *gombaszoegensis*, is in our opinion only attributable to *Panthera* sp. The family Mustelidae is added to the faunal list and includes *Martes* sp. and a smaller species. The presence of *Panthera leo* cf. *fossilis*, *Lynx pardina spelaea* and *Felis silvestris*, is confirmed. The presence of a not very speloid *Ursus deningeri*, together with the rest of the carnivore assemblage, points to a not very late Middle Pleistocene age, i.e., oxygen isotope stage 7 or older. Relative frequencies of skeletal elements for the bear and fox samples are without major biases. The age structure of the bear sample, based on dental wear stages, does not follow the typical hibernation mortality profile and resembles a catastrophic profile. The site was not a natal or refuge den. The hypothesis that the site was a natural trap is the most plausible. If the Sima de los Huesos functioned as a natural trap (without an egress out), the human accumulation cannot be attributed to carnivore activities and must be explained differently.

Introduction

The first study of the *Ursus deningeri* remains from the Sima de los Huesos site (in the Cueva Mayor cave, Sierra de Atapuerca), was carried out by Torres (1977), who recovered numerous bear fossils in his 1976 field season. Ceballos (1986), continued the study of the fossil bears, adding new material from the 1984 campaign. A comprehensive study of all the carnivore remains, excluding the ursids, from the Atapuerca sites Gran Dolina, Galeria and Sima de los Huesos, up to and including the 1982 field campaign, was published by Morales *et al.* (1987), including a first faunal list and description of the several taxa: Cuoninae indet., *Vulpes vulpes* sp., *Felis silvestris*, *Panthero leo* cf. *fossilis*, and *Panthera* cf. *gombaszoegensis*. Finally, Cervera (1992) reported on new findings of carnivore fossils, through the 1991 campaign, from the Sierra de Atapuerca site complex (excluding the Gran Dolina site), adding *Lynx pardina spelaea* to the SH list published by Morales *et al.* (1987).

The aim of this paper is update the carnivore fossil inventory through the 1995 field season, and to determine the biochronology of the site. A taphonomic study of skeletal part representation using bear and fox remains is performed, as well as a study of the bear sex distribution and mortality profile, in order to investigate the origin of the carnivore accumulation. Since the Sima de los Huesos contains the most complete sample of Middle Pleistocene humans yet discovered from one site, the origin of the carnivore accumulation reveals information also relevant as to human remains accumulated in the Sima de los Huesos site.

Material and methods

There are abundant *Ursus deningeri* remains of unequivocal taxonomic identification (Ceballos, 1986; Torres, 1988*a,b,c,d,e,f*). Before 1991 only carnivores from disturbed sediments were

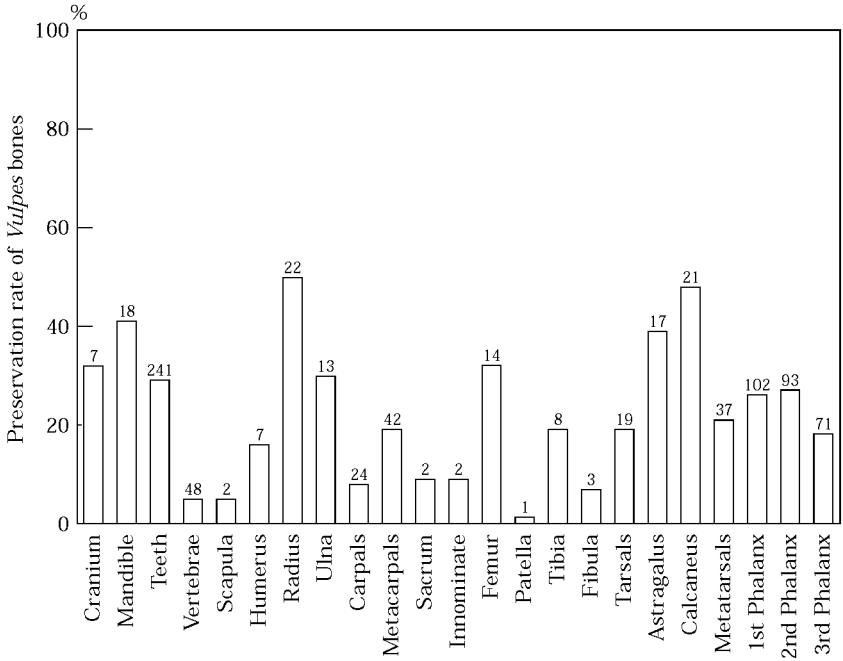


Figure 1. Preservation rate of cranial and postcranial fox bones from Sima de los Huesos. Percentages are calculated based on an MNI of 23 individuals. All skeletal parts are represented. The MNI for a particular skeletal element is calculated using that part of it (i.e., proximal end, distal end or shaft) that is more represented in the sample (on the left or right side) (following Lyman, 1994*b*). Numbers above each bar represent the actual number of specimens for each bone.

recovered in Sima de los Huesos (SH). Most of these fossils are fragmentary due to the activities of amateur collectors (Arsuaga *et al.*, 1997). In the 1989 and 1990 campaigns, undisturbed sediments were excavated in the more distal part of the site, but no carnivore fossils were found. From the 1991 campaign through the 1995 field season, many carnivore remains have been recovered from undisturbed sediments and we have used only this sample to study skeletal part representation. Following Ricklan (1986), we have also studied the relative preservation frequencies of podial elements, and since they are generally very well preserved, all podial elements recovered since the 1984 field season (in disturbed and undisturbed sediments) are used in this article. From 1990 to 1994, three test trenches in the Sala de los Cíclopes and Sala de las Oseras cave chambers (also in the Cueva Mayor cave) have been excavated, resulting in the recovery of more *U. deningeri* remains.

The *V. vulpes* sample is very large and a cumulative percentage graph (following Trinkaus, 1985 and Arsuaga *et al.*, 1990) and a bone preservation rate histogram provide insight to better understand the origin of the accumulation. We have also calculated the minimum number of individuals (MNI) for all taxa in SH, in each case using the most abundant anatomical part.

Inventories for all the taxa are provided in the text, and the bear and fox inventories are also presented in Figures 1–4. All measurements are to the nearest 0·1 mm.

Extant carnivores used for taxonomic identification were studied in the following collections: National Museum of Natural History, Smithsonian Institution: *Panthera leo*, adult individuals

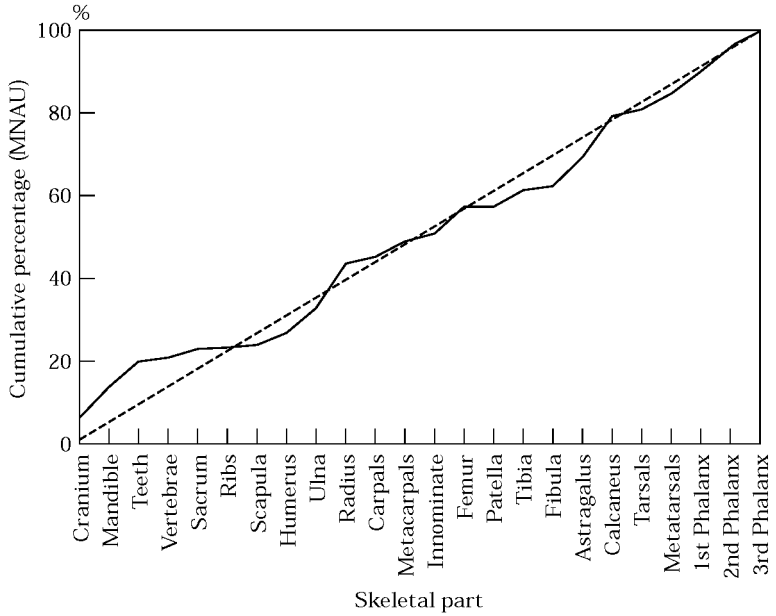


Figure 2. Cumulative percentage graph of minimum number of anatomical units of fox bones. (MNAU: number of bones or bone portions preserved in sample divided by number of that bone or bone portion in a complete skeleton. The MNAU percentage for each skeletal element is with respect to the total MNAU for the sample.) (——) Vulpes SH; (– – –) complete skeleton.

(postcranial, $n=8$; dentition, $n=14$); *Panthera pardus* (postcranial, $n=3$; dentition, $n=16$); *Panthera onca* (postcranial, $n=6$; dentition, $n=52$).

Museum of Vertebrate Zoology, University of California, Berkeley: a sample of five D^3 *Panthera leo* L. individuals used for comparison with the specimen from SH.

Estación Biológica de Doñana, Sevilla (C.S.I.C.): *Lynx pardina* (postcranial, $n=6$; dentition, $n=14$).

Departament of Vertebrate Zoology, Facultad de Ciencias Biológicas, Universidad Complutense de Madrid. *Canis lupus, V. vulpes, Felis silvestris.*

Facultad de Ciencias Biológicas de la Universidad Autónoma de Madrid. Mustelidae.

Felidae

Panthera leo *cf.* fossilis

Postcranial remains. One distal epiphysis of a tibia; one distal epiphysis of a radius; one proximal fourth of a radius; one proximal end of a second metatarsal; three tali; two calcanei; three scapholunars; two lateral cuneiforms; one third metacarpal; two fourth metacarpals; two third metatarsals; one sesamoid; five proximal phalanges; eight middle phalanges; one cervical vertebra; two caudal vertebrae.

Permanent dentition. Four M_1, four P_4, one P^4 and two P_3.

Deciduous dentition. Two upper canines, one D^3 and one D^4.

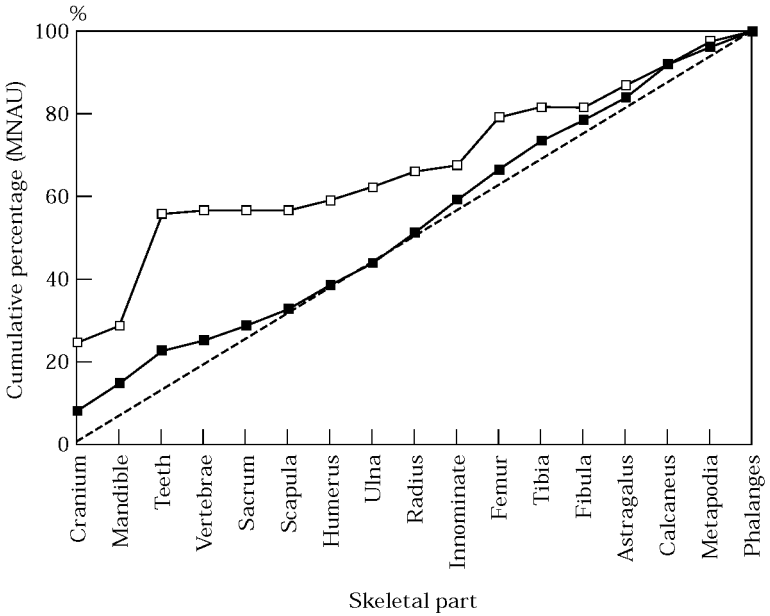


Figure 3. Cumulative Percentage Graph of minimum number of anatomical units in *U. deningeri* bones for the (■) SH sample, and (□) Westbury-sub-Mendip sample (Andrews & Turner (1992). (MNAU: calculated as in Figure 2.) (– – –) Complete skeleton.

Taxonomic assignation. We recovered four adult lower carnassials of *Panthera leo* cf. *fossilis* (Morales, 1987; Cervera, 1992) which are assigned to one male and one female (Figure 11) based on the pattern of sexual dimorphism in dental measurements of *P. leo* metric (Turner, 1984).

Furthermore, we have assigned a D^3 to a juvenile individual of the same species based on the measurements in Table 1. We assume that two upper deciduous canines and an upper D^4 belonging to a large felid that were recovered belong to the same immature individual (Figure 11). Thus, the MNI for this species is thus three.

Panthera *sp.*

Postcranial remains. Proximal two thirds of a left third metatarsal. It corresponds to a felid of considerably smaller size than *P. leo* cf. *fossilis*, and intermediate between *Panthera pardus* and *P. leo.* (Figure 10). Morales (1987) attributed this specimen to *Panthera* cf. *gombaszoegensis* based on its similarity to *Panthera onca augusta* dimensions (Kurtén, 1973). Nevertheless, Cervera (1992) only identifies *P. leo* cf. *fossilis* from the SH site because he considers the assignment of this metatarsal to a juvenile *P. leo* cannot be excluded. We see no juvenile features in the specimen but we prefer to refer to this specimen as *Panthera* sp., because although its measurements are very close to those of *P. onca augusta*, they are also close to large specimens of *P. pardus.*

Lynx pardina spelaea

Postcranial remains. One proximal fragment of a femur; one fragment of a scapula with glenoid fossa; one scapholunar; one metacarpal; one proximal phalanx; two middle phalanges.

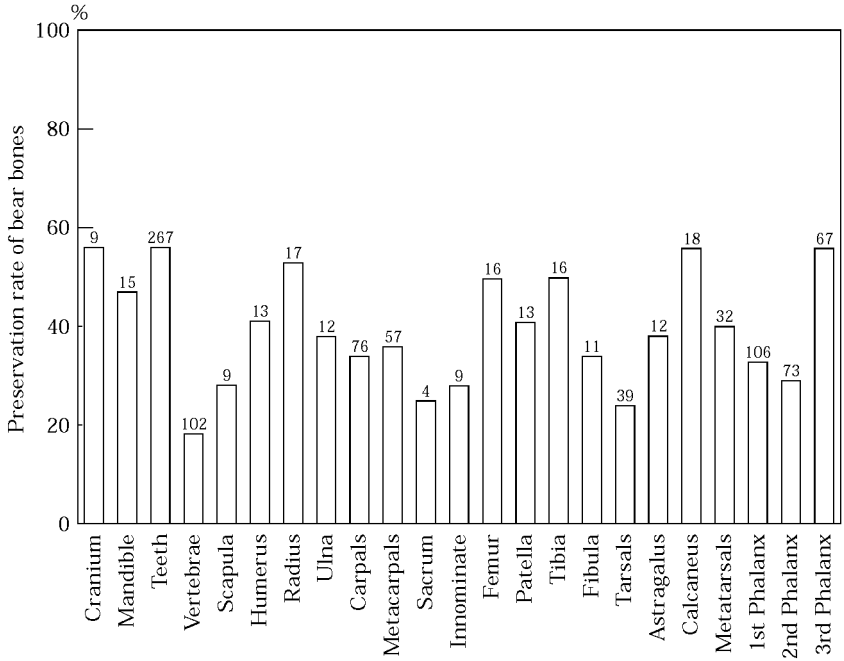


Figure 4. Preservation rate of cranial and postcranial bear bones from Sima de los Huesos. Percentages are calculated based on an MNI of 16 individuals. All skeletal parts are represented. The MNI for a particular skeletal element is calculated using that part of it (i.e., proximal end, distal end or shaft) that is more represented in the sample (on the left or right side). Numbers above each bar represent the actual number of specimens for each bone.

Table 1 D^3 measurements in modern lions compared with the SH specimen

	D^3 length		D^3 talon width	
	Mean	S.D.	Mean	S.D.
Panthera leo L. (extant) (*n*=5)	23·5	1·3	5·9	0·3
SH	24·8		6·4	

Cranial remains. Two associated hemimandibles from the SH undisturbed sediments. All teeth but the incisors are associated in place. An isolated lower canine was recovered in SRM. Thus, the MNI in the SH sample is two.

Taxonomic assignation. The Atapuerca (SH) lynx is a felid of medium size. The lower carnassials display morphological features typical of *Lynx pardina* differentiating it from *L. lynx*, such as complete absence of a metaconid and a talonid, and a protoconid with a straight posterior edge (Figure 11). Based on dimensions, this fossil is placed in the subspecies *L. pardina spelaea* (Werdelin, 1981; Cervera, 1992), a temporal variant, larger than the recent *L. pardina pardina*, and smaller than the Villafranchian species of southern Europe, *Lynx issidiorensis*.

Felis silvestris

Remains. One proximal phalanx, a distal epiphysis of a femur and one upper carnassial. MNI=1. The SH remains belong to a small-sized felid of similar morphology and measurements to the extant wild cat. A large P^4 is observed.

Mustelidae

Martes *sp. (Table 2)*

Postcranial remains. Four scapholunars; two os magni; one trapezium; two unciforms; one pyramidal; one calcaneus; one talus; one femur; one fragment of a scapula with glenoid fossa. The MNI is 3 based on the presence of three right scapholunars.

Dentition. One M^1, one P^4, four upper canines and three lower canines.

Taxonomic attribution. The attribution of these fossils to *Martes* is based on comparisons of the SH upper carnassial and first upper molar with Anderson's (1970) sample. Although many authors (Kurtén, 1965; Miller, 1912) have tried to establish metrical and morphological characters to distinguish the species of *Martes*, there is a large overlap between the ranges of *M. martes*, *M. foina* and *M. vetus* (the pine marten's probable ancestor) (Anderson, 1970) in the length and width of the protocone of the upper carnassial and the length and width of the inner lobe of the upper molar. In consequence, it is difficult to make a specific attribution on the basis of isolated teeth alone.

The most cited dental criterion is that the length of the upper carnassial (LP^4) is equal to the width of upper first molar (WM^1) in *M. martes* but is less than that in *M. foina* (Anderson, 1970). The Sima de los Huesos specimen shows an LP^4/WM^1 relationship like that in *M. martes* (Figure 10). To express this proportion metrically, we have calculated the LP^4/WM^1 and LP^4/LM^1 ratios using Anderson's means (Table 2). The upper teeth from SH are more similar to recent *M. martes* Postglacial *M. martes* and *M. vetus* than to *M. foina* values. In addition, the values of the LM^1/WM^1 ratio reveal that the SH specimen is closer to the recent and Postglacial *M. martes* populations, and the LP^4/LM^1 ratio shows more similarity between Recent *M. martes* and the SH specimen. Thus, the most likely assignation for these teeth is to *M. martes*.

Mustelidae *indet.*

Dentition. One P^4 and two M_1. MNI is 2.

Taxonomic assignation. These remains belong to a small mustelid, that might be attributable to *Mustela*.

Canidae

Canis lupus *(Table 3)*

Postcranial remains. One scapholunar; one lateral cuneiform; one pyramidal; four proximal phalanges; one middle phalanx; two fragments of two metapodials.

Table 2 Comparative measurements from Anderson (1970) including Danish recent *Martes martes*, Holocene *Martes martes* (from Danish Neolithic sites), recent Danish *Martes foina* and Middle Pleistocene *Martes vetus* (from the Sackdilling cave and Schernfeld sites)

	Martes foina ♂ (recent) ♀ n♂=56 n♀=10			*Martes martes* ♂ (recent) ♀ n♂=31 n♀=25			*Martes martes* ♂ (postglacial) ♀ n♂=7 n♀=4			*Martes vetus* nP^4=13 nM^1=13			*Mertes*
	Range	Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.	SH
LP^4 ♂	8·4–10	9·3	0·4	8·2–9·6	8·8	0·3	8·7–9·8	9·2	0·3				
										8·0–9·2	8·5	0·5	9·0
LP^4 ♀	7·7–9·0	8·5	0·3	7·5–8·9	8·1	0·4	7·4–8·5	7·9	0·4				
WM^1 ♂	7·9–9·3	8·7	0·4	8·1–9·2	8·8	0·3	8·1–9·4	8·9	0·5				
										6·9–9·0	8·0	0·5	9·2
WM^1 ♀	7·5–8·9	8·2	0·3	7·4–8·9	8·1	0·3	7·9–8·6	8·2	—				
LM^1 ♂	5·1–6·7	5·9	0·4	5·9–7·0	6·5	0·3	5·9–6·8	6·3	0·4				
										4·2–6·5	5·3	0·4	6·6
LM^1 ♀	4·4–5·7	5·2	0·4	5·5–6·5	5·9	0·3	5·6–6·0	5·6	—				
LP^4/WM^1 ♂		1·07			1·00			1·04					
											0·98		0·97
LP^4/WM^1 ♀		1·03			0·99			0·96					
LM^1/WM^1 ♂		0·67			0·74			0·71					
											0·61		0·71
LM^1/WM^1 ♀		0·63			0·72			0·67					
LM^1/LP^4 ♂		0·63			0·73			0·68					
											0·62		0·73
LM^1/LP^4 ♀		0·61			0·73			0·70					

S.D.=standard deviation, L=length, W=width.

Table 3 M_1 measurements of fossil wolves from the Lunel-Viel Middle Pleistocene site and SH

Character	*Canis lupus lunellensis* Lunel-Viel			*Canis lupus* SH	*Canis lupus* L. (extant)		
	n	Mean	S.D.	*n*=1	*n*	Mean	S.D.
Width M_1	11	9·9	0·42	10·3	10	11·4	0·5

Data from modern European wolves are taken from Miller (1912) cited in Altuna (1972), Altuna (1972) and from Kurtén (1965) and from Lunel-Viel from Bonifay (1971).

Table 4 P^4 and M^1 measurements of fossil foxes from the L'Escale Middle Pleistocene site and SH, and extant foxes from the Upper Peninsula of Michigan

Character	*Vulpes vulpes jansoni* L'Escale			*Vulpes vulpes* spp. SH			*Vulpes vulpes* recent		
	n	Mean	S.D.	*n*	Mean	S.D.	*n*	Mean	S.D.
Length P^4	7	13·9	0·3	10	14·6	0·5	48	13·9	0·5
Width P^4	6	6·7	0·6	10	6·5	0·5	50	7·3	0·4
Length M_1	6	15·6	0·7	24	15·7	0·8	50	15·4	0·7
Width M_1	5	5·8	0·4	23	5·8	0·5	48	5·8	0·3

Data from L'Escale are taken from Bonifay (1971) and from extaut foxes from Gingerich & Winkler (1979).

Dentition. One upper canine; a fragment of a canine crown; one M_1 (which preserves the trigonid cusps). These three pieces are at the same developmental stage, and we have assigned them to a single individual.

Taxonomic attribution. Based on the size of the postcranial bones, which are larger than *C. lupus lunellensis* from Lunel-Viel, Morales *et al.* (1987) assigned the following remains to *Cuoninae* indet.: B-763, B-4001, B-4002, B-4003, B-4004, B-4005 and B-4006. Later, a fragment of a left M_1 was found. A reduced and poorly defined metaconid is usually considered diagnostic of the genus *Cuon*. The SH lower carnassial shows a well-defined metaconid substantially larger than that of *Cuon alpinus europaeus* from the Middle Pleistocene Galeria site (also in Sierra de Atapuerca) (Figure 11). Comparison with *C. lupus lunellensis* from Lunel-Viel (Middle Pleistocene) shows that the Atapuerca SH M_1 is not larger (Table 3). Moreover, cuons and wolves from the Galeria site are similar in size (Figure 10).

Vulpes vulpes *(Table 4)*

The most common skeletal element in the SH assemblage of foxes is the right lower carnassial which gives an MNI of 23.

All remains recovered from the Sima de los Huesos site are similar in morphology and size to modern *V. vulpes* L. Measurements of the upper and lower carnassials are very close to those of *V. vulpes jansoni* from L'Escale (Table 4). Although the SH specimens have a larger upper carnassial, absolutely and relative to its width compared with a sample of North American fox or the Middle Pleistocene fox sample from L'Escale, we prefer not to assign the SH specimens to any subspecies, considering the wide size range of this species.

Ursus deningeri *Von Reich*

Taxonomic assignation of the Sima de los Huesos ursids is based on abundant postcranial and dental remains recovered during several campaigns (see Torres, 1977; Ceballos, 1985).

According to Prat (1976) *U. deningeri* only occurs in the Middle Pleistocene, becoming *Ursus spelaeus* in the late Middle Pleistocene. Bonifay (1975), considers the ursids from La Fage to be evolved (speloid). This site is stratigraphically assigned to Riss II and Riss II-III (broadly equivalent to oxygen isotope stages 8 and 7). To Arambourg (1958) and Bonifay (1975), the probably late Rissian (stage 6) sites of Fontéchevade yields a typical cave bear (*U. spelaeus*). In her paper of 1975, Bonifay considers *U. spelaeus* to succeed *U. deningeri* at the end of the Middle Pleistocene although Bonifay & Bussière (1989) classify as *U. deningeri* fossil remains from Aldène, from levels G and H assigned to the early Upper Pleistocene. Nevertheless, as Hennig (1982), on whose results they base their study, obtained radiometric ages which disagree with the biostratigraphical order, it is impossible to establish the chronology of these two layers. It just can be assumed that they are younger than marine isotope stage 9. The chronology of the transition *U. deningeri–U. spelaeus* is thus difficult to establish, in part because of the anagenetic nature of this evolutionary process, and in part due to the lack of an accurate geochronological framework for the late Middle Pleistocene sites. Auguste (1992) considers the ursids from Biache-Saint-Vaast, to be transitional between both species. This site has been dated by thermoluminescence to 175 ± 13 ka, and stratigraphic correlations with other sites place Biache at the end of the isotopic stage 7 (August, 1992); Yokoyama (1989) used gamma-ray spectrometry to obtain dates of $263+53-37$ ka (U-Th age) and >175 ka (U-Pa age) for the second human skull, and $182+46-31$ ka (U-Th) for an animal bone. Another site that can be used to date the *U. deningeri–U. spelaeus* transition is Lezetxiki. Here level VII (just above the level where a human humerus was found) yielded *U. deningeri* and two bone samples from this level have been dated to $309+\infty-92$ ka and $303+\infty-114$ ka (Altuna, 1992). In level VI ursids with more speloid traits are found and bone dates are $231+49-92$ ka and $200+129-58$ ka (Altuna, 1992). In sum, the pattern that emerges is a terminal Middle Pleistocene transition from *U. deningeri* to *U. spelaeus*.

In order to discuss the evolutionary position of the Sima de los Huesos ursids, it is necessary to analyze in detail the three distinct anatomical regions: cranial skeleton, postcranial skeleton and dentition.

Complete cranial remains are very rare due to the fragility of the skull; however, there are abundant mandibles. These present characters typical of an archaic representative of *U. deningeri* such as small size, mandibular ramus sloped posteriorly, straight inferior margin of the horizontal ramus (convex in the last representatives of *U. deningeri* and very convex in *U. spelaeus*, cf. Torres, 1978).

The most abundant complete remains of the postcranial skeleton are carpals, metacarpals, tarsals and metatarsals all of which show a primitive *U. deningeri* morphology. When compared with its ancestor, *Ursus etruscus*, this species shows a robustness increase of the postcranial skeleton, especially in the limb epiphyses, whereas the diaphyses remain slender. The first metacarpal and metatarsal are shorter and the articular facets of the carpal and tarsal bones are larger.

The dental formula of the SH *U. deningeri* is consistent with other Middle Pleistocene populations, such as Mauer, Mosbach and Petralona (Torres, 1988*e*). The SH bears commonly show the P_1 and P_3 which never occur in *U. spelaeus*.

Some primitive characters of *U. etruscus* (the last common ancestor of the arctoid and speloid lineages) are present in the SH ursid, such as the etruscoid morphology and size of P^4, P_4 and M_1, the reduced and rounded M_3, and an M^2 with a reduced, acute talon (Torres & Cervera, 1995). The metric and morphological patterns that characterize the *U. deningeri* population from SH do not correspond with transitional forms of *U. spelaeus* (Bonifay & Bussière, 1989), but with a typical representative of *U. deningeri*.

Aside from the systematic excavations at Sima de los Huesos, three test excavations were also carried out at two places in Sala de los Cíclopes and one place in Sala de las Oseras. These three chambers are inter-connected (Arsuaga *et al.*, 1997). In the lower part of Sala de los Cíclopes, *U. deningeri* remains (including two hemimandibles) were found. These fossils belong to a juvenile and an adult. At Sala de los Cíclopes, close to the Sima de los Huesos shaft, various other *Ursus deningeri* fossils were encountered, including the left hemimandible of a juvenile. Finally, in Sala de las Oseras some cranial and postcranial remains assignable to *Ursus deningeri* have been recovered.

Carnivore diversity

Some carnivore taxa are found in both SH and in the Galería complex (Middle Pleistocene), also in Sierra de Atapuerca: *P. leo fossilis*, *L. pardina spelaea*, *Felis silvestris*, *C. lupus*, *V. vulpes* and *Martes* sp. However, *U. deningeri* is not found in Galería. Some scarce remains were tentatively assigned to *U. spelaeus*. *Crocuta* is absent in Sima de los Huesos and represented in Galería only by an unerupted canine. A middle size felid (*Panthera* sp.), not found in Galería, occurs in SH. In sum, the carnivore taxonomic diversity found in SH is high, corresponding to a very productive milieu. An analysis of the pollen content of three samples taken in the clay matrix of human and bear fossils in Area A (Arsuaga *et al.*, 1997), showed that 40% of the grains (n=129) corresponded to tree pollen, with *Pinus*, deciduous *Quercus*, evergreen *Quercus*, *Betula* and *Fagus* in decreasing order of abundance (García-Antón, 1987). Communities with this tree species correspond to a climate something moister and colder than the current one in the Sierra de Atapuerca. It is striking the (cuasi) absence of specialized large scavengers as hyenas. According to Turner (1995) humans could have successfully competed with hyenas for this ecological niche in Spain during the Middle Pleistocene.

Taphonomical analysis of the bear and fox samples

The V. vulpes *bone accumulation*

The sample of foxes is large enough to allow study of the relative frequencies of skeletal elements. Figure 1 reveals that all cranial and postcranial bones are represented; the less frequent elements are the smallest and most fragile bones. Before the present study not all the skeletal elements of the small carnivores (i.e., foxes and mustelids) were systematically recovered in the laboratory among the thousands of bear bone fragments. Although we have resorted part of this material and found many previously unrecognized small carnivore bones, there is still a "laboratory bias" against the smallest or less diagnostic bones. Of the teeth recovered from the site, 59·1% (n=120) are mandibular teeth and 40·8% (n=83) maxillary teeth. Among the maxillary teeth, 51·8% come from the left side and 48·2% from the right side. Among the mandibular teeth, the numbers are 40·9% left and 59·1% right. A chi-square test shows a statistically significant bias (χ^2=6·74, P<0·01) in the upper teeth/lower teeth proportions in the sample, as well as in the carpal/metacarpal index (=24/42), but there is no

statistically significant bias ($\chi^2=0{\cdot}47$, $P>0{\cdot}25$) in the tarsal/metatarsal index (=57/37). Concerning side biases, the ratio of left upper teeth to right upper teeth (=43/40) does not significantly depart from a 1:1 ratio ($\chi^2=0{\cdot}1$, $P>0{\cdot}5$), whereas the left lower teeth/right lower teeth ratio (=49/71) departs significantly at the 0·05 level of probability but not at the 0·01 level ($\chi^2=4{\cdot}02$, $0{\cdot}05>P>0{\cdot}025$). In spite of the biases in some skeletal elements, that can be attributed to former "laboratory biases" or differential preservation of less structurally dense skeletal parts, and since there are no biases in other proportions and all the skeletal elements are present in the sample, without extreme bias, we consider that the most likely scenario is that complete foxes accumulated in the site.

Trinkaus (1985) and Arsuaga *et al.* (1990, 1995) used the cumulative percentage of the minimum number of anatomical units (MNAU) to express patterns of skeletal part preservation. The MNAU are calculated as "number of bones or bone portions preserved in sample divided by number of that bone or bone portion in a complete skeleton" and "the MNAU percentage for each skeletal element is with respect to the total MNAU for the sample (i.e., sum of all MNAU)" (Trinkaus, 1985; p. 210). We have applied the same method to the SH sample of foxes. The cumulative graph for *Vulpes* from the Sima de los Huesos (Figure 2) shows preservation of all skeletal elements without major bias. This also suggests to an accumulation of whole bodies in the Sima de los Huesos. The surfaces of the bones show no abrasion and therefore do not seem to have been subjected to significant fluvial transport.

Gargett (1994) discusses characteristics of bone accumulations expected in fox natal dens, refuge dens or natural traps. In a natal den we would expect to find the neonate age class represented predominantly, with all skeletal elements present (see also Blanco, 1988; Lauriño & Ruiz, 1986) and as well as remains of prey species (based on the analysis of excrements 90% of the diet of infant individuals in fox dens consists of vertebrates (Blanco, 1988)). A refuge den would be expected to contain a variety of scavenged or hunted animals and no fox bones; present day Spanish foxes show a slight predominance of rabbits in the diet (26%), fewer rodents (24%) and fewer birds (7%) (Blanco, 1988). In a natural trap situation, we would expect to find complete fox skeletons of all age classes, perhaps with the exception of neonates, and without associated prey species. Neonate remains have not been recovered (and a bias against them is rejected since small mustelid remains have been found as well as neonate bones of other taxa). Moreover, neither rabbits nor birds occur and there are only very few micromammals (Cuenca-Bescós *et al.*, 1997). Although in our opinion the data are more consistent with the trap hypothesis, a pattern of incidental deaths of foxes attracted into the cave by scavenging opportunities or going in for temporary shelter cannot be completely discarded.

The U. deningeri *bone accumulation*

In our taphonomic study of the bear fossils, we have chosen not to include data on specimens from sediments disturbed by many years of activities of amateur collectors looking for bear canines and other impressive fossils (Arsuaga *et al.*, 1997). The sample used in this analysis derives from *in situ* excavations in SH (areas A and B) and SRB between 1990 and 1995 (Arsuaga *et al.*, 1997, Bischoff *et al.*, 1997). The cumulative percentage graph (MNAU) shows preservation of all skeletal parts in both the SH (areas A and B) and the SRB excavation sites (Figure 3). Thus, we believe that the bear carcasses were complete when incorporated into this site. Although the cumulative percentage graph reflects the general pattern, and thus is not very sensitive to small biases or to biases that only occur in few elements, it does clearly show substantial differences between the very complete record of Sima de los Huesos, and sites such

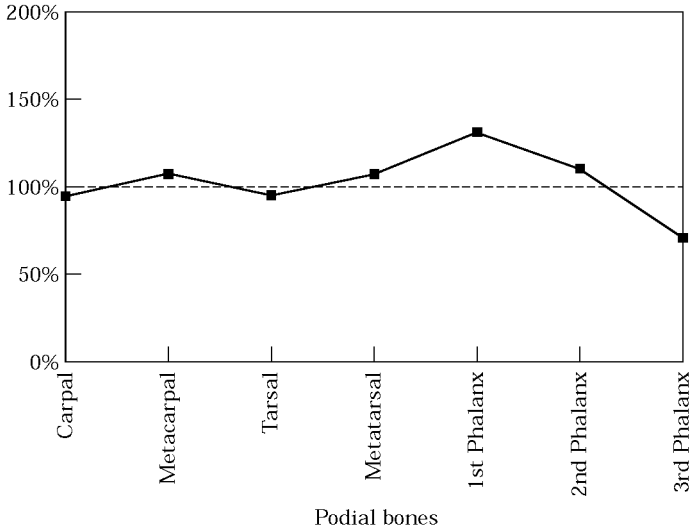


Figure 5. Relative preservation frequencies (RPF) of *U. deningeri* podials. No preservation cline from proximal to distal elements is observed.

as Westbury-sub-Mendip with more bias, where yet it is stated that complete skeletons went to the deposit (Andrews & Turner, 1992). A histogram of preservation rates of bear bones was calculated based on a MNI=16 (Figure 4) and there are no major biases.

The MNI was calculated using the most commonly occurring skeletal element in the whole SH assemblage, including in this instance the fossils from disturbed sediments. For adults the left upper second molar gives a MNI of 158 adult individuals. Using the right D_3, the MNI of immature individuals is 8.

The ratios (left:right) for fore- and hind-feet are 6:4 (n=367); metacarpals 4·6:5·4 (n=298); tarsals 5·1:4·9 (n=412); and metatarsals 5:5 (n=333). This indicates that there is no difference in the frequency of preservation of left and right elements. Of a total of 1410 podials recovered (excluding phalanges) the ratio for carpals+metacarpals *versus* tarsals+metatarsals is 4·7:5·3.

In contrast to Ricklan's (1986) results, no preservation cline in podials from proximal to distal elements is observed. Metacarpals and metatarsals are not better preserved by comparison with carpal and tarsal bones (χ^2 values of 1·8 and 2·34, respectively, both with probabilities >0·1), or phalanges, although there is a tendency for distal phalanges to be slightly less frequent in the material than proximal ones (Figure 5). Any bias against those elements have different density, mass, volume or size would exhibit such a clinical pattern if they had suffered transportation.

Mortality profiles. Dental development and attrition are used here to estimate age at death of the bears. Enamel attrition is used to estimate the age assuming a relatively constant wear rate in *U. deningeri* and *U. spelaeus*. Several authors have noted that these fossil bears can be grouped into clear-cut wear stages, corresponding to different ages. Since the bear fossils found in caves generally belong to individuals which died during hibernation, the wear stages thus analyzed are more discontinuous than in other carnivores that died throughout the year (Kurtén, 1958; Gargett, 1994; Musil, 1965; Andrews & Turner, 1992).

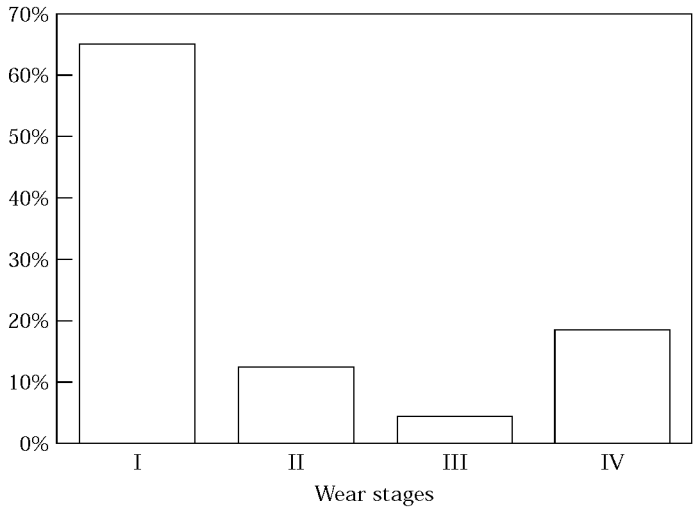


Figure 6. *Ursus spelaeus* mortality frequency histogram from Odessa. Wear determinations based on the upper second molar. Data from Kurtén (1958), $n=163$. A U-shaped pattern is observed.

We have investigated the tooth that occurs most frequently in the collection, the upper second molar, that begins to develop in the first year of life and extends into the early part of the second year. While Kurtén (1958) described six wear age stages, in this study we use only the four (Musil, 1965) that are clearly distinct. Furthermore we have included in Figure 8 the most abundant deciduous tooth (d_3) together with the four stages for permanent dentition, to show in a more graphic way the proportion of cubs with respect to juveniles and adults.

Stage I: Teeth with crown unworn, walls forming and roots still open at the apices (stages I and II of Kurtén).

Stage II: The roots are closed, the crowns started to be polished or even have a narrow attrition facet along the internal ridge but the cusps are clearly seen (stages III and IV of Kurtén).

Stage III: The facet is larger, extending to the occlusal surface of the crown with loss of a large part of enamel (stage V of Kurtén).

Stage IV: The facet is even more enlarged, the enamel has already disappeared through wear, and the cementum is eroded (stage VI of Kurtén).

The four wear stages are useful for interpreting the origin of the bear accumulation. Bears enter caves for hibernation and individuals that do not have sufficient fat reserves to subsist throughout the winter, are commonly very young or alternatively senile individuals (Kurtén 1958). Thus, the mortality profile expected for bears dying during hibernation is an attritional pattern, with the juvenile and senile groups best represented, in a bimodal, or "U-shaped" distribution (Klein, 1984; Lyman, 1994*a*). That is the pattern found in *Ursus spelaeus* from Odessa (Kurtén, 1958) (Figure 6) and from Reguerillo (Torres, 1974) (Figure 7).

By contrast a catastrophic mortality pattern is non-selective, and is described as a frequency distribution of age classes in which successively older age classes are represented by fewer individuals, with a unimodal or "L-shaped" frequency distribution (Klein, 1984; Lyman, 1994*a*). The large *U. deningeri* sample from Sima de los Huesos shows a mortality frequency histogram that does not correspond to the attritional distribution but does conform to the

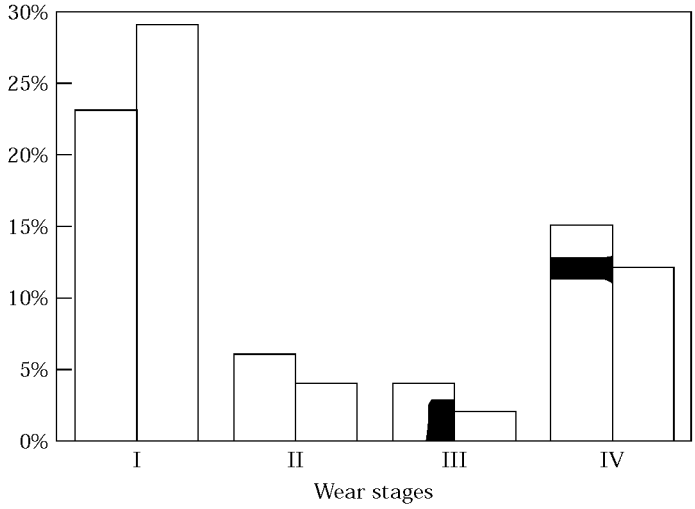


Figure 7. *Ursus spelaeus* mortality frequency histogram from El Reguerillo. Wear determinations based on the upper second molar. Data from Torres (1976), $n=107$. A U-shaped pattern is observed. (▨) Left; (□) right.

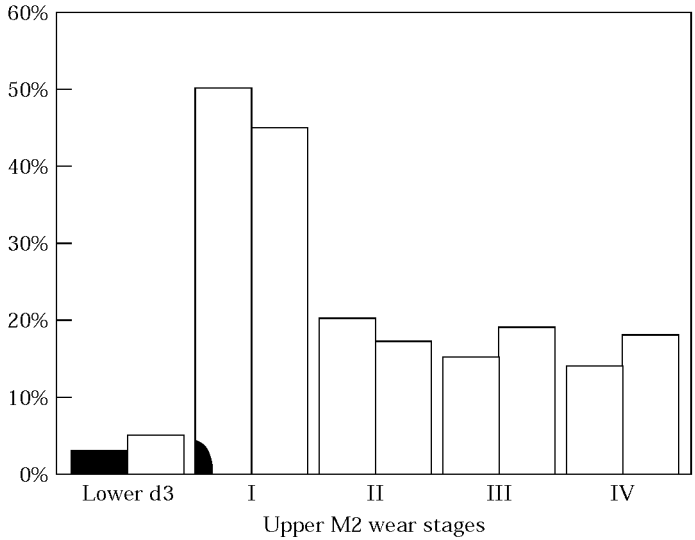


Figure 8. *Ursus deningeri* mortality frequency histograms from Sima de los Huesos. Wear determinations based on the upper second molar. Data from Ceballos (1986), Torres (1988*a*) and our data $n=291$. The pattern is L-shaped. At the left side of the graph, a frequency histogram of the most abundant milk tooth (d_3) of bear cubs younger than nine months shows the proportion of cubs with respect to juveniles and adults, $n=13$. (▨) Left; (□) right.

catastrophic type (Figure 8). A Kolmogorov–Smirnov test performed between the SH and the Odessa samples, although not conclusive ($D=0{\cdot}16$, $0{\cdot}05>P>0{\cdot}01$), shows that the SH profile is unusual for a hibernation derived sample. Fossils of *U. deningeri* have also been found in Cueva Mayor, in Sala de los Cíclopes and Sala de las Oseras, as well as in hibernation beds. These chambers are connected to the Sima de los Huesos through a 13 m deep shaft

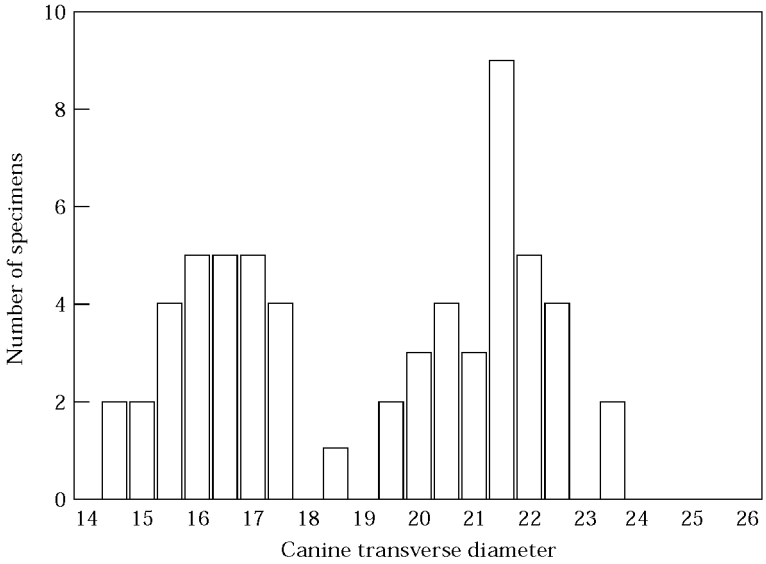


Figure 9. Frequency distribution of lower canine width in *Ursus spelaeus* from Odessa (n=63). Note the bimodal distribution with lower values attributable to females and higher ones to males.

(Arsuaga *et al.*, 1997) and it is possible that some of the bears that came into these cavities to hibernate fell down into the Sima de los Huesos, perhaps over a long period of time. On the other hand, the hypothesis that the SH accumulation corresponds to a place where bears hibernated and females gave birth, accessing the site through a passage (unknown) other than the shaft, is not consistent with the low neonatal (less than 1 year old) proportion (eight out of 166, only the 4·8% of the total SH sample) relative to some *Ursus spelaeus* sites, such as Odessa, which neonatal mortality rate is about 40% of individuals (Kurtén, 1958). Although very young individuals have admittedly less resistant bones, milk teeth are generally preserved in the sites, and in the Sima de los Huesos site milk teeth have been always sorted out when the sedimentary matrix is sieved looking for micromammals, so that recovery bias is excluded.

Sex ratio

Following Kurtén (1969), we have used the width of the canine crown to separate males and females. A bimodal distribution is expected for a representative sample of sexually dimorphic species such as cave bears (Kurtén, 1969). Lower values are attributable to females and higher ones to males (Figure 9). The SH sample of *U. deningeri* is positively skewed, with its mode at the 15 mm class (Figure 10) and a substantially smaller peak to the right (mode at the 19 mm class). It seems that females hibernated in this part of Cueva Mayor, some of which fell into the Sima de los Huesos, more frequently than males. Other similar cases of unbalanced sex ratios have been described for *U. deningeri* and *U. spelaeus*, and were explained by Kurtén (1958) as due to a preference by females to hibernate in a cave not occupied by other bears. The reason for this would be the possible dangerous behavior of male bears to their offspring, and in an easily defended position.

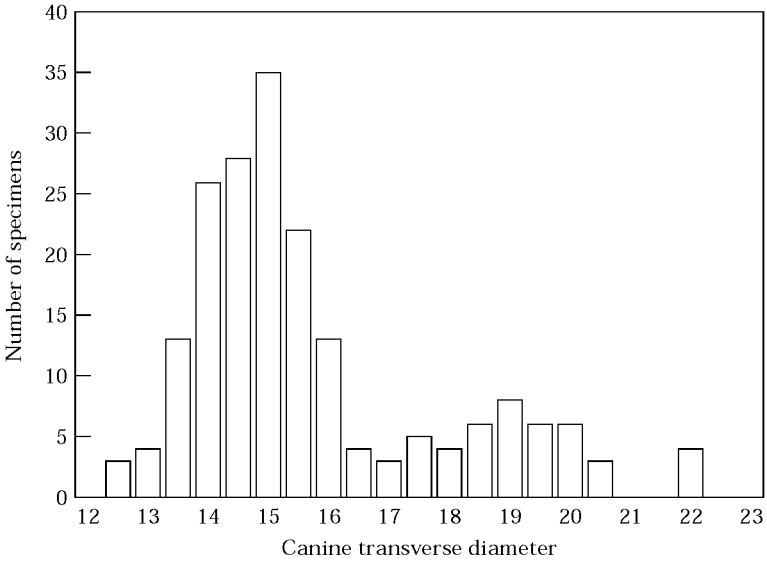
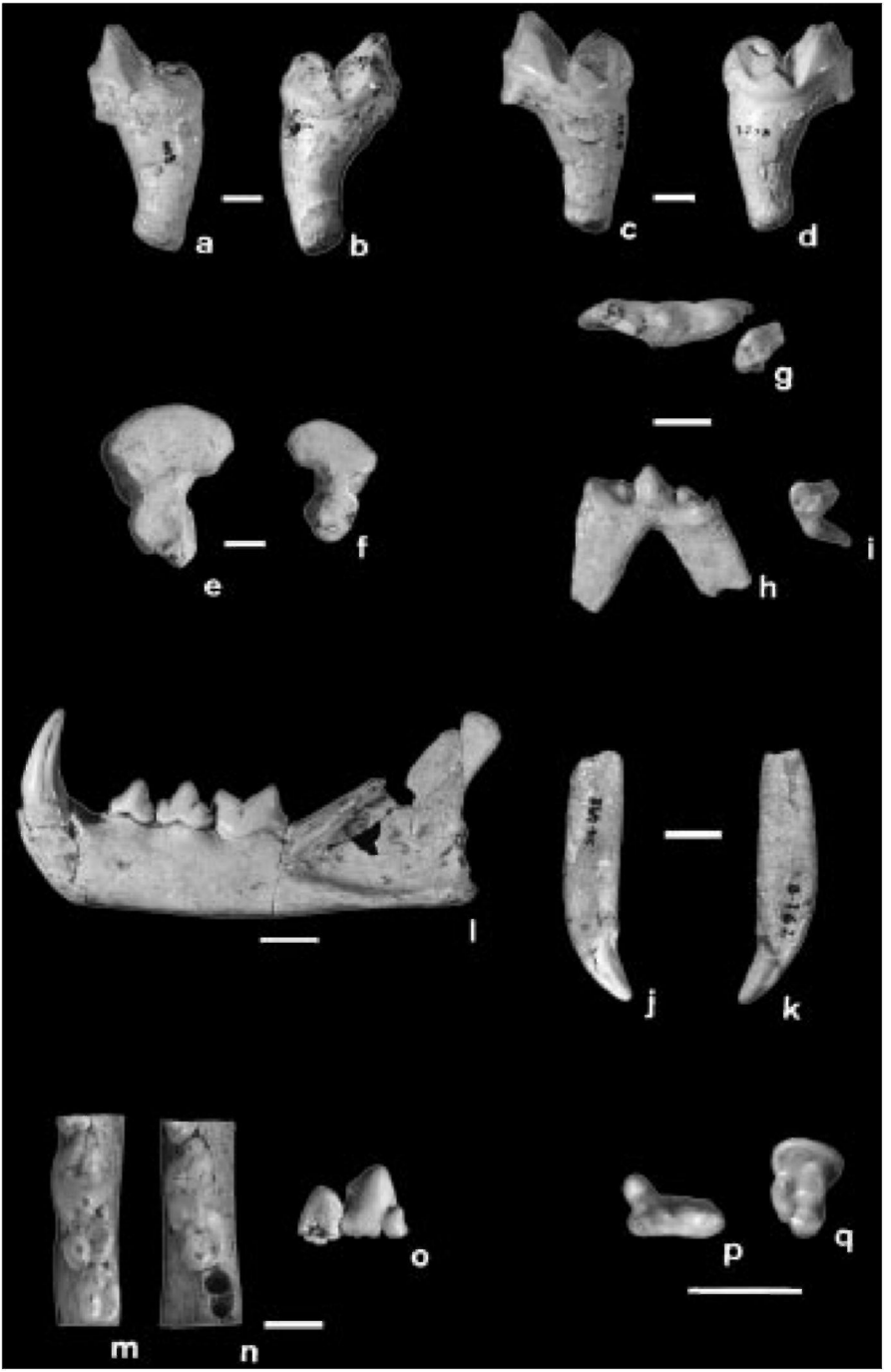


Figure 10. Distribution of canine width in *Ursus deningeri* from Sima de los Huesos. Data from Ceballos (1986), Torres (1988) and our data (n=164 teeth). Note that the distribution is positively skewed, with a mode at the 15 mm class and a substantially smaller peak to the right.

Summary and conclusions

The fauna of the Sima de los Huesos site in Cueva Mayor is biased in that it consists of very few micromammal (Cuenca-Bescós *et al.*, 1997), carnivores and human remains. There is a large number of *U. deningeri* (MNI=158). A few remains of one individual of a large-sized wolf are present, whereas *V. vulpes* is relatively abundant (MNI=23). Several differently sized felids, such as *P. leo.* cf. *fossilis* (MNI=3), *Panthera* sp. (MNI=1), *L. pardina spelaea* (MNI=2) and *Felis silvestris* (MNI=1), are each represented by a few remains. There are also several mustelids, of two different sizes. No herbivores have been found. The SH carnivore sample corresponds to a typical Middle Pleistocene carnivore guild, with the exception of hyaenids, which are altogether lacking. Remains of *U. deningeri* are also abundant in the Sala de los Cíclopes and Sala de las Oseras chambers of Cueva Mayor, cavities to which the Sima de los Huesos site is connected through a 13 m deep shaft.

Figure 11. Carnivore remains from the SH site. (a) and (b) right and left lower carnassials; respectively of *P. leo* cf. *fossilis*, labial view; (c) and (d) right and left lower carnassials; respectively of *P. leo* cf. *fossilis*, lingual view; (e) and (f) proximal views of a right third metatarsal of *P. leo* cf. *fossilis* (e) and a left third metatarsal of *Panthera* sp. (f). Note the substantial size difference between the two. (g) Left D^3 and D^4 of *P. leo* cf. *fossilis*, occlusal view. (h) Left D^3, labial view; same tooth as in (g). (i) Left D^4; same tooth as in (g). (j) and (k) Left and right upper decidual canines of *P. leo* cf. *fossilis*, lingual view. (l) Left hemimandible of *L. pardina spelaea*, labial view. Note the absence of a metaconid in M_1 and that the protoconid has a straight posterior edge. (m) and (n) Occlusal views of the left M_1 of *C. lupus* (m) and *Cuon alpinus europaeus* (n) from Trinchera site. Note the similarity in size. (o) Right fragment of M_1 of *Canis lupus* from SH, lingual view. Note the large metaconid observed in (m) and (o) compared with the very reduced one in (n). (p) Right P^4 of *Martes* sp., occlusal view. (q) Left M^1 of *Martes* sp., occlusal view. Scale bar represents 1 cm.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The unbiased skeletal part representation of bears and foxes indicates an accumulation of whole carcasses in Sima de los Huesos. Bears probably made use of the Cueva Mayor, and hibernated in Sala de los Cíclopes and Sala de las Oseras, but the *U. deningeri* mortality profile in Sima de los Huesos, calculated from dental wear stages, does not follow the attritional model expected under hibernation circumstances. The predominant wear stage is attributable to approximately 2 year old juveniles. Senile individuals are less well represented. Moreover, neonates are proportionally very rare. So we do not consider hibernation as the cause of death. If there was another entrance to the Sima de los Huesos (i.e., different from the shaft) in the Middle Pleistocene, the other carnivores could theoretically have made occasional use of SH as a den. However the absence of prey and carnivore neonates leads us to discard both possibilities. Finally, carnivores could have been attracted by the carrion at the site or for temporary shelter and incidentally they could have died. There is no way to know if the carnivores died trapped or "naturally". Nevertheless, the large number of foxes (more than 23) suggests a trap. The larger the number of foxes in the accumulation, the more unlikely is the natural death hypothesis. Moreover, the Sima de los Huesos has served as a death trap for small carnivores until the present (Arsuaga *et al.*, 1997).

In sum, in our opinion, the carnivores did not have easy access to and exit from the site cavity. The most likely scenario compatible with the structure of the Sima de los Huesos carnivore assemblage is a natural trap (very likely the current pitfall) attracting carnivores to accidental deaths. This scenario is not compatible with carnivores being the accumulating agency for the human remains. Human corpses had to accumulate under other circumstances (Arsuaga *et al.*, 1997).

The *V. vulpes* from SH does not differ morphologically and metrically for *Vulpes vulpes jansoni* of L'Escale (Middle Pleistocene) or from extant populations, although the LP^4/WP^4 ratio is slightly larger in the SH sample.

Skeletal remains previously assigned to Cuoninae indet. are now classified as *Canis lupus* based on the recovery of additional remains. The size of this canid is greater than *Canis etruscus* from L'Escale or *Canis lupus mosbachensis* and is similar to *Canis lupus lunellensis* from the Lunel-Viel Middle Pleistocene site.

The carnivore assemblage of the Sima de los Huesos, containing among other taxa, a well documented and relatively primitive form of *Ursus deningeri*, is compatible with the upper Middle Pleistocene age suggested by the geochronological dating (Bischoff *et al.*, 1997) and the biostratigraphic conclusions based on micromammals (Cuenca-Bescós *et al.*, 1997). In particular, the presence of an archaic form of *U. deningeri* (i.e., not transitional to *U. spelaeus*), together with the rest of the carnivore assemblage, points to an isotope stage 7 age or (probably) older.

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